Title

Assisted gene flow in the context of large-scale forest management in California, USA

Journal

Ecosphere, 11(1)

ISSN

2150-8925

Authors

Young, DJN
Blush, TD
Landram, M
et al.

Publication Date

2020

DOI

10.1002/ecs2.3001

Peer reviewed

Running head

Assisted gene flow in forest management

Title

Assisted gene flow in the context of large-scale forest management in California, USA

Authors and affiliations

Derek J. N. Young[†]**:** Department of Plant Sciences, University of California, Davis, California; djyoung@ucdavis.edu

Thomas D. Blush: Retired, USDA Forest Service, Pacific Southwest Region, Vallejo, California

Michael Landram: Retired, USDA Forest Service, Pacific Southwest Region, Vallejo, California

Jessica W. Wright: USDA Forest Service, Pacific Southwest Research Station, Davis, California; jessicawwright@fs.fed.us

Andrew M. Latimer: Department of Plant Sciences, University of California, Davis, California; amlatimer@ucdavis.edu

Hugh D. Safford: USDA Forest Service, Pacific Southwest Region, Vallejo, California, and Department of Environmental Science and Policy, University of California, Davis, California; hughsafford@fs.fed.us

[†]Corresponding author

24

Abstract

As climate changes, locally adapted tree populations may become maladapted to the sites in which they presently occur. When natural adaptive processes are insufficient for populations to keep pace with changing climate, human-assisted relocation of genotypes (“assisted gene flow”) may be a useful tool for maintaining forest resilience. While existing empirical evidence provides insight into the potential outcomes and consequences of assisted gene flow, its applicability to large-scale plantings needs to be evaluated. We conducted a test of assisted gene flow in the context of operational post-fire restoration plantings in three United States Department of Agriculture National Forests in California. Our experimental restoration plantings included seedling provenances representing both the local planting site and lower elevation provenances that may be adapted to hotter and drier conditions. For the duration of the experiment, the planting sites experienced anomalously hot, dry conditions, offering a window into the potential outcomes of assisted gene flow in a future climate characterized by warmer temperatures and more frequent drought. In most cases, there was no significant difference in seedling growth or survival among provenances. However, in a few cases, lower-elevation provenances performed better than local provenances, suggesting a potential benefit of assisted gene flow as a management response to climate change. Our analyses accounted for spatial variation in shrub cover and detected a consistent and substantial negative association between shrub cover and seedling growth. In addition, our study

revealed that the use of operational seed collections that are not geographically precise (and therefore also not climatically precise) can complicate selection of appropriate provenances and lead to unpredictable outcomes. Numerous other risks and uncertainties—including the fact that tree populations are often adapted to local site factors other than climate and that long-term outcomes may differ from short-term observations—complicate evaluations of the potential utility of assisted gene flow.

Keywords: Climate change, adaptation, tree, forest, restoration, assisted gene flow

Introduction

Seed source selection

Tree planting can be an important component of forest management and restoration, particularly following severe wildfires and intensive timber harvest (McDonald and Fiddler 2010). When planning tree planting projects, managers select sources (e.g., collection locations or specific parent trees) for the tree seeds that are used. Based on a long history of studies that often identify strong local adaptation in tree populations (Langlet 1971, Conkle and Critchfield 1988, Ying and Liang 1994, Howe et al. 2003, St Clair et al. 2005, Kitzmiller 2005, Wright 2007, Savolainen et al. 2007), many forest managers have historically prioritized the use of seeds collected from near the planting site while also incorporating a reasonable range of genetic variation (Ledig

and Kitzmiller 1992). This approach helps to ensure that most of the planted trees are well-adapted to the environmental conditions of the planting site and that planted populations maintain adaptive capacity in future generations (Savolainen et al. 2007, Alberto et al. 2013). Matching seed source and planting site environment often results in increased performance of planted trees relative to alternative approaches that do not carefully account for the provenance of planted trees (Langlet 1971, Aitken and Bemmels 2016).

Appropriate seed source selection methods are less clear when environmental conditions are changing. Given a scenario of progressive warming and drying, for example, it may make sense to select seeds from source environments that are hotter and drier than the planting site, as genotypes from those environments may be better adapted to certain environmental conditions (e.g., frequent drought) that may eventually characterize the planting site (Aitken and Whitlock 2013). The approach of intentionally moving genotypes of a given species to new locations within the species range in order to track changing environmental conditions is referred to as “assisted gene flow” (Ledig and Kitzmiller 1992, Aitken and Whitlock 2013). Assisted gene flow differs from “assisted migration” (also known as “assisted colonization” or “managed relocation”) (McLachlan et al. 2007) in that the latter concepts include managed relocation of individuals or populations of a species beyond the species’ historic geographic range limit as opposed to moving them within the existing species range. However,

many of the same motivations, guiding principles, and cautions apply to both assisted gene flow and assisted colonization (Aitken and Whitlock 2013).

Empirical evidence of assisted gene flow outcomes

Under changing climatic conditions, local adaptation to current climate implies maladaptation to future climate (Aitken and Bemmels 2016), suggesting to some extent that populations may perform better if relocated to new sites. However, many of the same reciprocal transplant studies that identify local adaptation also highlight important potential negative consequences of assisted gene flow, particularly when populations are adapted to additional local factors beyond climate (Bucharova 2017; also see Discussion).

Despite the large body of literature on common garden and provenance tests, only a few empirical studies to date have directly evaluated the outcome of assisted gene flow—that is, specifically moving genotypes into sites where the environment has changed to more closely match the relocated genotype's historical source environment (or at least some component of it) (Bucharova 2017). One study tested assisted gene flow in a tree species (*Populus tremuloides* Michx.) that the authors suggest has experienced substantial adaptive lag over a long period of historical climate warming, such that most populations now occur in a climate substantially warmer than that to which they are adapted (Schreiber et al. 2013). That study observed substantial improvements in growth and survival

in populations that were moved northward into colder sites, without accompanying indications of cold-related maladaptation, representing potential positive outcomes of assisted gene flow.

Other studies have taken an alternative approach, using periods of anomalously hot weather (Hancock and Hughes 2014, Bucharova et al. 2016) to test applications of assisted gene flow. In contrast to expectations, these studies found that with only a few exceptions, individuals from local populations performed as well as or better than individuals from warmer provenances (i.e., candidate populations for relocation), even under anomalously warm conditions. This unexpected result may potentially be explained by the fact that the studies only evaluated adaptation to temperature (as opposed to other potentially important climatic factors such as moisture availability) and were conducted over a single growing season with plants that began < 1 year old, despite all study species being perennials.

An operational forest management context

Despite growing recognition of the potential importance of assisted gene flow in forest management, existing studies of assisted gene flow have (a) been performed under highly controlled conditions that may not be representative of operational forest management and (b) yielded contradictory and unexpected results (see previous section). We sought to evaluate the potential outcomes of assisted gene flow applied in large-scale

post-fire forest restoration plantings and gain insight into potential limitations or other considerations unique to implementation of assisted gene flow in an operational context. To this end, we studied post-fire plantings of five different tree species conducted by the USDA Forest Service (USDA-FS) at three sites in California. The challenges faced by the USDA-FS in California (e.g., responsibility for managing a large and environmentally-heterogeneous forested region given limited resources) are not unique, so we use the California plantings as a case study of assisted gene flow implementation and outcomes potentially relevant to any institution responsible for managing a large and climatically-diverse forested region.

When replanting following severe wildfire, many management agencies, including the USDA-FS Pacific Southwest Region (which includes California), use seedlings grown from seed that was previously collected and then stored in a seed bank in anticipation of a future reforestation need. In the USDA-FS Pacific Southwest Region seed bank, an individual accession is referred to as a “seed lot” and is identified by the seed zone and 500-ft-wide (~150-m-wide) elevation band (e.g., “4000-4500 ft elevation”) from which seeds were collected (Fig. 1; Table 1; Appendix S1: Figs. S1-S6). Similar collection and cataloging systems are used by other large forest management agencies—for example, the California Department of Forestry and Fire Protection, or “Cal Fire” (Stewart McMorrow, Cal Fire Deputy Chief of Forestry Assistance, *personal communication*).

The California tree seed zones are variable in size, averaging roughly 30-50 km in latitude and longitude, and are intended to define regions with relatively consistent climatic and physiographic conditions (Buck et al. 1970). The reason for delineating seed lots based on seed zone and elevation band is to maintain separate collections of seed representative of specific local environmental (including climatic) conditions. A given USDA-FS seed lot may consist of seeds collected from one or more trees (generally 1 to 4) in each of one or more stands (usually 5 to > 20) throughout the geographic region defined by the seed lot's seed zone and elevation band (Table 1). Collections have historically prioritized more stands vs. more trees per stand in order maximize diversity (Arnaldo Ferreira, Geneticist, USDA-FS Pacific Southwest Region, *personal communication*).

USDA-FS seed lots are less geographically and climatically specific than the provenances typically used in research studies of local adaptation and assisted gene flow. However, they reflect the current reality of large-scale forest management. To gain realistic insight into the potential role of assisted gene flow in large-scale management practices (e.g., the management practices of the USDA-FS), it is thus essential to evaluate (a) the selection and performance of provenances as defined by management agencies (e.g., USDA-FS seed lots) and (b) the degree to which the use of geographically imprecise seed lots constrains the potential for implementation of assisted gene flow in an operational context.

In the present study, we evaluate the growth and survival of seedlings that originated from seed lots that are representative of the planting site, as well as seed lots representing lower elevations, at three sites that were planted following severe wildfire. For the duration of this experiment, California experienced a drought so extreme it had no historical precedent (Robeson 2015). The drought offers the potential opportunity to gain insight into expected outcomes of assisted gene flow in an overall hotter and more variable future climate. We additionally evaluate the limitations of relying on operational seed lots with imprecise collection location data, and we interpret our results (as well as implementation and expected outcomes of operational assisted gene flow in forests generally) in this context.

Methods

Experimental design

We worked with three U.S. National Forests (Appendix S1: Table S1) to establish experimental tree plantations in the spring of 2011 during operational restoration planting in areas that had recently experienced high-severity wildfire. At each of the three planting sites (i.e., National Forests), seedlings from multiple provenances of one or more species (Table 1) were planted in a randomized complete block design. The provenances planted were unique to each site; that is, each provenance was only planted at one of the three planting sites (Table 1). However, we used the same treatment group types (i.e., one local and one or two lower-elevation provenances) at

each of the three planting sites. At each site, we established three experimental blocks, each containing all provenances of each species tested at the site. Because the sites were planted by operational tree planting crews, the use of fewer, larger blocks (as opposed to more, smaller blocks) was necessary to ensure accurate planting and tracking of the multiple species and provenances.

Across all three sites, the species planted were: Douglas-fir (*Pseudostuga menziesii* [Mirb.] Franco*),* incense cedar (*Calocedrus decurrens* [Torr.] Florin), ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), Jeffrey pine (*Pinus jeffreyi* Balf.), and sugar pine (*Pinus lambertiana* Douglas). We used these species because they were present on each respective site prior to wildfire and they were the same species being used for operational post-fire reforestation in the burned areas surrounding the experimental study plots.

In total, 147 USDA-FS nursery-grown seedlings (49 seedlings per block x 3 blocks) of each provenance of each species were planted at each site. Seedlings were planted in a contiguous spatial arrangement with 2 to 3 m between each tree. At this spacing, competition among these small trees should be minimal (Cole and Newton 1987). At the Plumas and San Bernardino sites, seedlings were planted in a separate 7 x 7 grid for each provenance and replicate. At the Klamath site, seedlings were planted in a wheel-and-spoke design (Nelder 1962) with 12 spokes, a center tree, and four trees per spoke (12 x 4 +1=49). This design was favored by the local

manager because once the trees are much larger it will allow for evaluation of competition at a range of densities. At each site, the relative positions of each provenance cluster were randomized across blocks. Additional plantings were conducted at a fourth site (the Angeles National Forest), but one block of seedlings was inaccessible due to extremely high density of a hazardous plant (*Eriodictyon parryi* [A. Gray] Greene) so the site was excluded from this study. However, the plantings remain for future monitoring. Competing vegetation was manually removed from within at least 30 cm of each planted tree during planting at each site to reduce competitive/facilitative impacts. At the San Bernardino site, the existing vegetation (primarily shrubs) was masticated across the entire planting area and the masticated material was left on the site. In early 2015 at the Klamath site only, newly recruited competing vegetation was again manually removed from within at least 1 m of most planted trees.

Provenances were selected to represent scenarios of upslope assisted gene flow and status-quo management. At each site, one provenance of each species that was planted originated from the same 500-ft elevation band as the planting site (or, in the specific case of ponderosa pine planted at the Klamath site, the 500-ft elevation band below the planting site) (Table 1). The high-elevation provenance was intended to reflect status-quo management in which seeds are sourced from as close to the planting site as possible. The remaining planted provenance(s) of each species originated

from elevation band(s) 500 to 3500 ft (~150 to 1050 m) lower (Table 1), representing scenarios of assisted gene flow.

Field measurements

We measured the experimental seedlings twice: once in September 2012 after two growing seasons in the field, and once in September 2015, three years later. In 2012, we measured all surviving planted seedlings at the Klamath and San Bernardino sites and a random sample of one third of all surviving planted seedlings (due to time constraints) at the Plumas site (Table 1: # of seedl.). In 2015, we re-measured (or recorded mortality of; Table 1) all previously measured seedlings that (a) were not beneath an object such as a fallen log, (b) had no apparent severe mechanical damage (e.g., from a rolling log), (c) were not apparently killed by a burrowing mammal, and (d) could be confidently identified to a specific seedling measured in 2012. Seedlings not meeting these criteria were excluded from the dataset. We additionally tested excluding seedlings with signs of animal browsing, but we found that this did not qualitatively influence inferences or conclusions (results not shown). We therefore included browsed seedlings in the analyses we report here in order to reflect the reality of operational forest management.

In both surveys (initial and final), we measured the height and basal diameter of each seedling. In the final survey, we also visually estimated the percent cover by shrubs of the area within 1 m of each seedling. We

estimated percent cover in categories (0%, 0-1%, 1-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-90%, and 90-100%) and used the middle value of each category for statistical analyses. This approach requires confident knowledge of the location of a seedling. We were unable to precisely locate many dead seedlings, so we could not confidently estimate shrub cover surrounding them. We therefore did not include shrub cover in survival analyses. We estimated the stem volume of each tree at each time point based on the tree's height and basal diameter, modeling the stem as a cone (Broncano et al. 1998). We only measured aboveground morphology, but incorporating basal diameter into the growth metric may additionally capture aspects of belowground morphology better than height alone (Marx et al. 1977, Dey and Parker 1997).

Identifying provenance and planting site climates

Because specific collection locations within a given seed zone-elevation band combination are unknown, we present the climatic range of potential collection locations within each experimental provenance (USDA-FS seed lot) as a range (Table 1) and as a point cloud (Fig. 2) representing the climate across the region defined by the seed lot's seed zone and elevation band. To do so, we first defined the geographic region from which seeds in each seed lot may have been collected by using geospatial layers of seed zones (Eldorado National Forest, Geographic Information Services, *personal communication*), and elevation (USGS 2018) (Fig. 1; Appendix S1: Figs. S1-

298S6). Within the resulting region, we placed a grid of points with 100 m-by-
299100 m spacing and computed temperature and precipitation values at each
300point using the gradient-inverse distance squared (GIDS) statistical
301downscaling method (Nalder and Wein 1998) as modified by Flint and Flint
302(2012). We obtained normal mean annual temperature and normal total
303annual precipitation during the 1981-2010 reference period from the ~800
304m-resolution TopoWx dataset for temperature (Oyler et al. 2014) and the
305~800 m-resolution PRISM dataset for precipitation (PRISM Climate Group
3062019). We chose to use these relatively simple climate variables because (a)
307they are easily obtained and used in management applications and (b) within
308small regions typical of our analysis (e.g., Fig. 1), spatial variation in annual
309temperature and precipitation is highly correlated with spatial variation in
310many other biologically-relevant climate variables (De Clercq et al. 2015).
311 We also quantified the climates of the planting sites (Fig. 2; Table 1).
312We identified the normal climate over the 1981-2010 period by extracting
313values at planting site locations using the modified GIDS downscaling
314method from the same TopoWx and PRISM layers used to define the climates
315of the seedling provenances. Additionally, to represent the climate during
316the 4-year period that the seedlings were growing in the field, we computed
317mean annual temperature during the October 2011—September 2015 period
318from monthly ~800 m-resolution TopoWx temperature layers (Oyler et al.
3192014) and mean annual total precipitation over the same period from
320monthly ~4 km-resolution PRISM layers (PRISM Climate Group 2019) and

extracted values at planting site locations using the same modified GIDS downscaling method.

Statistical analyses

To test for differentiation in seedling growth and survival among the provenances (seed lots) of each species, we developed statistical models that use initial (2012) observations to establish a baseline that accounts for variation due to nursery and planting practices (Jacobs et al. 2005), and the change between measurements (2012 to 2015) to identify variation potentially attributable to provenance differences. Specifically, for seedling growth, we fit hierarchical Gaussian (normal) linear models to explain final (2015) stem volume using initial (2012) stem volume, shrub cover, and provenance. This modeling approach allowed us to evaluate the effect of seedling provenance on final seedling size, independent of the influence of initial seedling size and shrub cover. We treated provenance as a categorical variable, with 1 or 2 dummy variables for species with 2 or 3 provenances, respectively. We always considered the high-elevation (local) provenance as the “baseline” provenance represented by the intercept of the model (as opposed to a dummy variable), as this was the provenance representing status-quo management. We allowed the model’s intercept and coefficient(s) for provenance dummy variable(s) to vary randomly across experimental blocks to account for block effects and for the existence of multiple experimental units (trees) within each block-by-provenance combination

(Quinn and Keough 2002). The survival models thus effectively incorporate a random intercept for each data row (i.e., block-by-provenance combination of survival/mortality counts), which additionally serves to account for any overdispersion in the data (Elston et al. 2001, Agresti 2002). Prior to fitting models, we log-transformed initial and final stem volume values in order to satisfy assumptions of normality, and we standardized continuous predictor variables by subtracting the mean and dividing by the standard deviation (separately for each site-by-species combination).

We fit a separate model for each site-by-species combination. The model specification given tree *i* within experimental block *j* for a site-by-species combination with two provenances is as follows:

$$\text{final\_volume}_i \sim N(\mu_i, \sigma^2)$$

$$\mu_i = \beta_{0j[i]} + \beta_{1j[i]} \bullet \text{provenance\_low}_i + \beta_2 \bullet \text{initial\_volume}_i + \beta_3 \bullet \text{shrub\_cover}_i$$

$$\beta_{0j[i]} \sim N(\mu_{\beta 0}, \sigma_{\beta 0}^2)$$

$$\beta_{1j[i]} \sim N(\mu_{\beta 1}, \sigma_{\beta 1}^2)$$

We repeated the same modeling procedure for survival between initial (2012) and final (2015) surveys, except that we used a binomial response distribution (with a logit link) and did not include shrub cover or initial stem volume as predictors. We excluded shrub cover because it was often impossible to precisely locate the planting locations (and thus quantify the surrounding shrub cover) of dead seedlings. It was not possible to fit survival models for ponderosa pine at the Klamath site or for Jeffrey and sugar pines

at the Plumas site, either because survival was consistently very high (Plumas species; Table 1), or because one experimental block contained too few seedlings to achieve robust model fits (Klamath ponderosa pine).

To visualize differences in seed lot growth and survival among provenances, we used fitted models to predict final stem volume and survival for a hypothetical "average" experimental block, average shrub cover, and average initial stem volume. To do so, in making model predictions, we held shrub cover and initial stem volume explanatory variables constant at their means for each respective site-by-species combination, and we held all effects that vary by block at zero. We randomly sampled 1000 sets of model fixed-effect coefficients using the fitted multivariate normal distribution of coefficients. For each set of coefficients, we predicted the response (stem volume or survival probability) for each provenance, and we then computed the median and 95% confidence interval of the responses across all 1000 sets of coefficients (Gelman and Hill 2007, McElreath 2016). We additionally computed pairwise contrasts (the difference in predicted response value and associated 95% confidence interval) between all provenance pairs for each site-by-species combination using the same sets of sampled model coefficients. We performed all statistical analyses in R version 3.4.1 (R Core Team 2018) using the package 'lme4' (Bates et al. 2015) for fitting generalized linear mixed-effects models.

Results

Provenance and planting site climates

The geographic region from which seeds of a given provenance were reported to have been collected (based on the recorded seed zone and 500-ft elevation band of the corresponding seed lot) was generally very broad (e.g., Fig. 1; Appendix S1: Figs. S1-S6). Mean climate generally varied widely across space within each of these regions (Fig. 2). For example, the high-elevation seed lots of Douglas-fir and incense cedar planted at the Klamath site (defined by seed zone 301 and the 4500-5000 ft elevation band) encompassed a region with normal annual precipitation ranging from under 1200 mm to nearly 4000 mm and normal mean annual temperature ranging from 8.1 °C to 10.2 °C (Fig. 2). Most other provenances evaluated in the experiment also originated from seed lots representing regions that encompass a > 2-fold range in mean annual precipitation and a 2-4 °C range in mean temperature (Fig. 2).

Source precipitation and temperature values also differed among provenances of a given species, to varying extents (Fig. 2). The among-provenance differentiation is driven by geographic variation in climate, with cooler, wetter conditions generally more common at higher elevations and in more coastally-influenced regions. However, the ranges of precipitation values overlapped substantially among provenances, despite the fact that the elevation limits of all provenances were separated by at least 500 ft (Table 1). For example, for Douglas-fir planted at the Klamath site, the potential source precipitation range for the high-elevation seed lot was 1170-

413 3986 mm, for the mid-elevation seed lot was 888-3732 mm, and for the low-
414 elevation seed lot was 875-3184 mm (Table 1). Potential source temperature
415 ranges were generally more clearly differentiated among provenances,
416 though overlap did occur to some extent (Fig. 2). The overlap was generally
417 greater for provenances from elevation bands that were closer in elevation
418 (e.g., Plumas species and Klamath ponderosa pine; Table 1).

419 The normal climate of the planting sites (i.e., the mean annual
420 temperature and total annual precipitation over the 1981-2010 reference
421 period) generally fell within the climate space of potential seed collection
422 sites of the high-elevation provenance for each species and site combination
423 (Fig. 2). At each planting site, the climate during the 4-year duration of the
424 experiment was substantially hotter and drier than the long-term average
425 climate (Fig. 2). As a result, in most cases the climate conditions at the
426 planting site during the experiment fell within the climate space of potential
427 seed collection sites of a lower-elevation provenance planted at the site.

428

429 *Provenance performance*

430 In several cases, the low-elevation provenances out-performed the
431 high-elevation provenances in terms of growth and/or survival, but in most
432 cases the differences were not individually significant for a given species at a
433 given site (Figs. 3-4; Appendix S1: Table S2). Performance among
434 provenances differed significantly only for incense cedar planted at the
435 Klamath site and for Jeffrey pine planted at the San Bernardino site. For

incense cedar, the low-elevation provenance had significantly larger model-predicted final stem volume (mean 30 cm^3) than both the mid-and high-elevation provenances (mean 14 cm^3 and 16 cm^3 stem volumes, respectively), accounting for differences in starting size and shrub cover (Fig. 3; Appendix S1: Table S2). Additionally, both the low- and high-elevation provenances of incense cedar had significantly higher model-fitted survival rates (mean 92% and 97%, respectively) than the mid-elevation provenance (73%; Fig. 4; Appendix S1: Table S2).

As with the incense cedar at the Klamath site, the low-elevation provenance of Jeffrey pine at the San Bernardino site had a significantly larger model-predicted final stem volume (mean 200 cm^3) than the high-elevation provenance (126 cm^3; Fig. 3; Appendix S1: Table S2). The low-elevation provenance also had a significantly higher model-predicted survival rate (mean 98%) than the high-elevation provenance (mean 92%; Fig. 4; Appendix S1: Table S2).

With few exceptions, in models that included shrub cover as a predictor of stem volume, shrub cover was significantly and substantially negatively associated with final stem volume (Table 2). The only exceptions were the individual species-by-site models for two species at the Klamath site, where shrubs had recently been manually removed from within approximately 1 m surrounding each tree.

Discussion

Differentiation in performance among some provenances

In two separate cases (Klamath incense cedar and San Bernardino Jeffrey pine), seedlings from a lower-elevation provenance exhibited greater growth and survival than the high-elevation provenance that was selected to reflect status-quo local seed sourcing (Figs. 3-4; Appendix S1: Table S2). Within a given seed zone, lower elevations are most often climatically hotter and drier than higher elevations (though there are many exceptions; Fig. 2), so the stronger growth of the low-elevation provenances (also seen in all other species and sites, but not significantly) may reflect adaptations to the anomalously hot, dry conditions that prevailed at the (higher-elevation) planting site for the duration of the experiment. This observation aligns with other observations of local adaptation along climatic gradients in pine species in California (e.g., Kitzmiller 2005), including Jeffrey pine (Martínez-Berdeja et al. 2019); however, we note that there is a lack of existing data for incense cedar. Our observation also aligns with the conceptual notion that in a future with hotter temperatures and more frequent drought, assisted gene flow has the potential to yield increased tree growth and survival relative to status-quo management (Aitken and Whitlock 2013).

Faster growth and greater short-term survival relative to other provenances may not, however, necessarily reflect better adaptation to the conditions at a site. Plants from warmer provenances are often observed to grow faster than plants from cooler provenances, even when planted into cooler environments (Mangold and Libby 1978, Morgenstern 2011). This

observation may be attributed to a tradeoff between growth rate and cold hardiness (Loehle 1998, Koehler et al. 2012), as trees that invest in cold hardiness (e.g., increased solute accumulation and delayed bud break) have fewer resources available for growth. Thus, although warmer- and wetter-provenance trees may grow faster than local trees, they may suffer more extensive damage in rare cold or dry events that are not captured in short-term studies like ours.

Notably, the mid-elevation seed lot of Klamath incense cedar showed significantly lower survival than either the low-elevation or high-elevation (local) incense cedar seed lots, thus providing an important counterexample to the idea that upslope assisted gene flow leads to stronger performance. This observation may be a consequence of the limited geographic specificity of seed lot collection locations: the potential climatic range from which the seeds may have been collected includes conditions very distinct from the planting site's climate (see *Limited geographic specificity of seed collection locations*, below).

It is also possible that the provenance differentiation we observed was driven by non-genetic factors such as differential treatment of the seedlings in the nursery (Jacobs et al. 2005) and maternal provisioning (Roach and Wulff 1987), but our model, which accounts for "initial" size and survival after one year of growth in the field, should help to rule out (but potentially not completely exclude) such effects.

Limited differentiation in performance among other provenances

Growth and survival were not significantly different among provenances for the remaining site-by-species combinations that we tested, although most combinations trended toward greater growth in low-elevation seed lots. This limited differentiation was unexpected given that local adaptation along environmental gradients, even at relatively fine scales, is often observed for many of the species in our study, including Douglas-fir (Campbell 1979, St Clair et al. 2005), ponderosa pine (Kitzmiller 2005), and sugar pine (Eckert et al. 2015).

The lack of significant differentiation in our study could be due to several factors. First, we may simply not have had enough statistical power to detect these differences. The planting sites reflect actual post-fire conditions in which tree planting is conducted, and these conditions are variable. Our models detected and accounted for a generally strong negative influence of shrub cover on seedling growth (Table 2), consistent with results of manipulative studies in this system that identify strong competitive effects of shrubs both aboveground (i.e., for light) and belowground (i.e., for water and/or nutrients) (e.g., Conard & Radosevich, 1982). However, there are numerous other sources of potentially important environmental variation, including shrub height and species identity, soil characteristics, and microenvironments created by logs and other objects (Gray and Spies 1997, Gray et al. 2005). This variability reflects the reality of managed landscapes, and in this regard our results reflect the outcomes that may be expected in a

management context. Progressively increasing the sample size would eventually almost always achieve significance (Quinn and Keough 2002), but our sample sizes are already sufficient for detecting differences that are large enough in magnitude to be relevant in the context of post-fire management (Table 2).

Limited geographic specificity of seed collection locations

Another potential explanation for the lack of substantial provenance differentiation is the uncertainty about the exact collection location and, therefore, the source climate of each provenance. USDA-FS seed lot designations (i.e., the intersection of the recorded seed zone and 500-ft elevation band) can cover wide geographic areas and a large range of climates (Fig. 1; Appendix S1: Figs. S1-S6). Without any further information, the seeds of a given seed lot may have been collected from one extreme of the potential geographic/climatic space, the opposite extreme, or anywhere in between—each leading to different expectations of relative provenance performance. Further, seed lots often consist of seed collections from multiple locations (stands) within a seed zone and elevation band (Table 1). In all of the cases in which our study identified seed lot performance differentiation (growth and survival of Klamath incense cedar and San Bernardino Jeffrey pine), the potential source climate range of the best-performing provenance does not even include the planting site climate. Further, in the case of Klamath incense cedar survival, the potential source

climate range of the *worst*-performing (mid-elevation) provenance *does* contain the planting site climate. Given the large range of potential source climate of each seed lot, it may be the case that seeds from the poorly-performing seed lots were actually collected from a region of their potential climate space that was more dissimilar to the planting site than the collection locations of the other seed lots, potentially explaining the stronger performance of the other seed lots.

Our analyses further demonstrate that given limited information about collection locations, common assumptions (e.g., that lower-elevation provenance climates are warmer and drier) are not necessarily valid. All else equal, lower elevations are, indeed, generally hotter and drier than higher elevations. However, when comparing low- and high-elevation points at different locations within a seed zone, this pattern does not always hold. In fact, in comparing two 500-ft elevation bands separated by even 1000 ft or more of elevation, some sites in the higher-elevation band can actually be hotter and drier than some sites in the lower-elevation band (Fig. 2). This issue is exacerbated when comparing elevation bands from disparate seed zones.

Dependence on seed lots collected and/or cataloged with limited geographic specificity is a challenge common to many large land management institutions beyond the USDA-FS Pacific Southwest Region (e.g., Cal Fire; Stewart McMorrow, Cal Fire Deputy Chief of Forestry Assistance, *personal communication*). Given available staff and financial

resources, it is infeasible to store, track, and manage seed collections from individual source trees separately (Sara Wilson, former Seed Bank Manager, USDA-FS Pacific Southwest Region, *personal communication*). This reality highlights the fact that many principles of seed lot selection and assisted gene flow that are proposed and evaluated in the academic literature may not be directly applicable to large-scale management scenarios. It also highlights the importance of updating management practices to address the challenges of climate change.

Options for revising management practices include requiring greater geographic specificity when collecting and cataloging seeds (e.g., recording geographic coordinates of each parent tree or collection site), maintaining individual seed collections separately rather than pooling them (even when they originate from the same seed zone and elevation band), and developing quantitative seed transfer guidelines that incorporate empirical data on the climatic (and other environmental) tolerances of species and populations as well as expectations of climate change and associated uncertainty. Management agencies including the USDA-FS; Cal Fire; and the British Columbia, Canada, Ministry of Forests are already prioritizing many such revisions (Arnaldo Ferreira, Geneticist, and Sara Wilson, former Seed Bank Manager, USDA-FS Pacific Southwest Region, *personal communications*; Stewart McMorrow, Cal Fire Deputy Chief of Forestry Assistance, *personal communication*; Snetsinger 2004, O'Neill et al. 2017). Tools to facilitate climate-based seed transfer of precisely-located seed collections have

recently been developed (e.g., the Seedlot Selection Tool; seedlotselectiontool.org).

Nuances, challenges, and risks of implementing assisted gene flow

It is possible that even small provenance differentiation will affect performance in the long term despite being less apparent in early years (Schuler 1994, Rice and Knapp 2008), when growth rates are relatively low and microenvironments can have a large influence (Gray and Spies 1997). This interpretation is supported by our observation that the species trial exhibiting the most growth by far (Jeffrey pine at the San Bernardino site) also showed significant provenance differentiation. Adaptive differentiation among provenances when trees are younger or smaller may be realized in phenotypic attributes that we did not measure, including phenology, freezing tolerance, xylem density, and rooting depth (Aitken and Adams 1997, Oleksyn et al. 1999, St Clair et al. 2005). While the seedling stage is often considered the most sensitive to environmental stress (Grubb 1977)—and thus potentially the most likely to exhibit performance differentiation—it is possible that any signals of environmental maladaptation were dampened by planting vigorous nursery-grown seedlings (Ledig and Kitzmiller 1992). To the extent that this is the case, it highlights the fact that planting tree seedlings can exclude opportunities for natural selection, and it emphasizes the importance of carefully selecting the genotypes used for seedling planting projects (Millar and Libby 1989).

620 An additional challenge in implementing assisted gene flow is that we
621often hope for the trees we plant today to persist on a site for decades to
622centuries, but climate change is expected to present a continuously moving
623target for at least decades to come (Aitken & Bemmels, 2016). Thus,
624assisted gene flow may require choosing between (a) planting trees that may
625be well-adapted in the future but are not at present or (b) vice-versa. Given
626the potential for limited cold-hardiness in heat- and drought-adapted
627populations (Loehle 1998, Koehler et al. 2012), it may be advantageous to
628wait to move hot- and dry-provenance genotypes into historically cooler,
629wetter sites *in response to* (not *in anticipation of*) climate change, when rare
630cold events may be less common. This approach would only be effective,
631however, to the extent that trees can persist through some amount of
632climate change in their present sites.
633 Existing provenance studies—particularly those that involve planting
634trees of a given provenance into multiple environments—can also help to
635identify the extent to which provenances can be safely transferred in
636anticipation of future warming (Hufford and Mazer 2003). For example, a
637transplant study in *Populus fremontii* S. Watson determined that the spatial
638seed transfers necessary so that trees planted today are well-adapted in 100
639years would result in substantially reduced performance today (Grady et al.
6402015). Ironically, the trees that can tolerate the largest transfers today in
641anticipation of future climate change (i.e., those that are the least

642climatically-sensitive) may be the most able to tolerate climate change in the
643absence of assisted gene flow (Wang et al. 2006).

644 Additional risks surround implementation of assisted gene flow.
645Introgression between local and introduced populations could result in
646outbreeding depression (Weeks et al. 2011, Aitken and Whitlock 2013);
647alternatively, reproductive phenological mismatches between local and
648introduced genotypes could prevent desirable introduced alleles from
649establishing in the local population (Wadgymar and Weis 2017). Populations
650of tree species, including some of the species we studied, often exhibit local
651adaptation to factors that do not vary with climate (e.g., soil properties,
652photoperiod, pathogens, and mutualists) (Wright 2007, Putten 2012,
653Kranabetter et al. 2012, Way and Montgomery 2015, Grady et al. 2015),
654likely impacting the success of populations relocated specifically to track
655climate (Schiffers et al. 2013, Bucharova 2017). The existence of these other
656adaptations may provide an alternative explanation for our unexpected
657observations. Existing common garden studies designed to evaluate the
658extent of local adaptation to individual environmental attributes (e.g.,
659climate or soil type) provide an important foundation for predicting outcomes
660of assisted gene flow. However, the most directly relevant information comes
661from studies that explicitly compare performance of relocated vs. local
662genotypes under altered climate. Such studies are relatively rare (Schreiber
663et al. 2013, Hancock and Hughes 2014, Bucharova et al. 2016).

While results of existing and future research can help guide assisted gene flow decisions, there will always exist some uncertainty regarding the best tree provenance(s) for any given application. Uncertainty exists due to imperfect information regarding many important factors, including future climate, likelihood of introgression and outbreeding depression, and extent of local adaptation to non-climatic factors. Given this reality, assisted gene flow programs could be designed around a “composite provenancing” approach (Broadhurst et al. 2008) in which multiple provenances—each of which might potentially be appropriate under different assumptions—are combined. Such approaches, however, should account for the possibility of increased mortality (due to trees that prove to be maladapted; Ledig and Kitzmiller 1992) in determining planting densities and future follow-up management. Additional research into the potential outcomes and consequences of assisted gene flow—including studies of the climatic tolerances of tree populations and the strength of adaptation to non-climatic biophysical factors that trees may experience differently if relocated—could meaningfully inform seed selection decisions.

Acknowledgments: We thank the local USDA Forest Service staff who coordinated installation of the experiments and facilitated monitoring: R. Tompkins, L. Smith, J. Hooper, C. Stith, and T. Drake. We also thank the dedicated field technicians who assisted with monitoring: J. Borba, A. Le, B. Baatar, and A. Merritt. We gratefully acknowledge funding from the USDA

Forest Service Region 5 Ecology Program. Finally, we thank the two anonymous reviewers whose comments substantially improved this manuscript.

Data archiving statement: Data for this study are available at [to be completed after manuscript is accepted for publication].

References

Agresti, A. 2002. Categorical Data Analysis, Second Edition. Wiley & Sons, Inc., New York, NY.

Aitken, S. N., and W. T. Adams. 1997. Spring cold hardiness under strong genetic control in Oregon populations of Pseudotsuga menziesii var. menziesii. Canadian Journal of Forest Research 27:1773–1780.

Aitken, S. N., and J. B. Bemmels. 2016. Time to get moving: assisted gene flow of forest trees. Evolutionary Applications 9:271–290.

Aitken, S. N., and M. C. Whitlock. 2013. Assisted Gene Flow to Facilitate Local Adaptation to Climate Change. Annual Review of Ecology, Evolution, and Systematics 44:131010123440000.

Alberto, F. J., S. N. Aitken, R. Alía, S. C. González-Martínez, H. Hänninen, A. Kremer, F. Lefèvre, T. Lenormand, S. Yeaman, R. Whetten, and O. Savolainen. 2013. Potential for evolutionary responses to climate change - evidence from tree populations. Global Change Biology 19:1645–1661.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67.

Broadhurst, L. M., A. Lowe, D. J. Coates, S. A. Cunningham, M. McDonald, P. A. Vesk, and C. Yates. 2008. Seed supply for broadscale restoration: maximizing evolutionary potential. Evolutionary Applications.

Broncano, M. J., M. Riba, and J. Retana. 1998. Seed germination and seedling performance of two Mediterranean tree species, holm oak (shape

718 Quercus ilex L.) and Aleppo pine (shape Pinus halepensis Mill.): a
719 multifactor experimental approach. Plant Ecology 138:17–26.
720Bucharova, A. 2017. Assisted migration within species range ignores biotic
721 interactions and lacks evidence. Restoration Ecology 25:14–18.
722Bucharova, A., W. Durka, J.-M. Hermann, N. Hölzel, S. Michalski, J. Kollmann,
723 and O. Bossdorf. 2016. Plants adapted to warmer climate do not
724 outperform regional plants during a natural heat wave. Ecology and
725 Evolution 6:4160–4165.
726Buck, J. M., R. S. Adams, J. Cone, M. T. Conkle, W. J. Libby, C. J. Eden, and M.
727 J. Knight. 1970. California tree seed zones. San Francisco: California
728 Region, Forest Service, U.S. Department of Agriculture; 5 p.
729Campbell, R. K. 1979. Genecology of Douglas-fir in a watershed in the
730 Oregon Cascades. Ecology 60:1036–1050.
731Cole, E. C., and M. Newton. 1987. Fifth-year responses of Douglas-fir to
732 crowding and nonconiferous competition. Canadian Journal of Forest
733 Research 17:181–186.
734Conard, S. G., and S. R. Radosevich. 1982. Growth Responses of White Fir to
735 Decreased Shading and Root Competition by Montane Chaparral
736 Shrubs. Forest Science 28:309–320.
737Conkle, M. T., and W. B. Critchfield. 1988. Genetic variation and hybridization
738 of ponderosa pine. Pages 27–43 *in* D. M. Baumgartner and J. E. Lotan,
739 editors. Ponderosa Pine: The Species and Its Management. Washington
740 State University Cooperative Extension Service, Pullman, WA.

De Clercq, E. M., S. Leta, A. Estrada-Peña, M. Madder, S. Adehan, and S. O. Vanwambeke. 2015. Species distribution modelling for Rhipicephalus microplus (Acari: Ixodidae) in Benin, West Africa: Comparing datasets and modelling algorithms. Preventive Veterinary Medicine 118:8–21.

Dey, D. C., and W. C. Parker. 1997. Morphological indicators of stock quality and field performance of red oak (Quercus rubra L.) seedlings underplanted in a central Ontario shelterwood. New Forests; Dordrecht 14:145–156.

Eckert, A. J., P. E. Maloney, D. R. Vogler, C. E. Jensen, A. D. Mix, and D. B. Neale. 2015. Local adaptation at fine spatial scales: an example from sugar pine (Pinus lambertiana, Pinaceae). Tree Genetics & Genomes 11:42.

Elston, D. A., R. Moss, T. Boulinier, C. Arrowsmith, and X. Lambin. 2001. Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. Parasitology 122:563–569.

Flint, L. E., and A. L. Flint. 2012. Downscaling future climate scenarios to fine scales for hydrologic and ecological modeling and analysis. Ecological Processes 1:2.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevelhierarchical models. Cambridge University Press New York, NY, USA.

762Grady, K. C., T. E. Kolb, D. H. Ikeda, and T. G. Whitham. 2015. A bridge too
763 far: cold and pathogen constraints to assisted migration of riparian
764 forests. Restoration Ecology 23:811–820.
765Gray, A. N., and T. A. Spies. 1997. Microsite controls on tree seedling
766 establishment in conifer forest canopy gaps. Ecology 78:2458–2473.
767Gray, A. N., H. S. J. Zald, R. A. Kern, and M. North. 2005. Stand conditions
768 associated with tree regeneration in Sierran mixed-conifer forests.
769 Forest Science 51:198–210.
770Grubb, P. J. 1977. The Maintenance of Species-Richness in Plant
771 Communities: The Importance of the Regeneration Niche. Biological
772 Reviews 52:107–145.
773Hancock, N., and L. Hughes. 2014. Turning up the heat on the provenance
774 debate: Testing the ‘local is best’ paradigm under heatwave
775 conditions. Austral Ecology 39:600–611.
776Howe, G. T., S. N. Aitken, D. B. Neale, K. D. Jermstad, N. C. Wheeler, and T. H.
777 Chen. 2003. From genotype to phenotype: unraveling the complexities
778 of cold adaptation in forest trees. Canadian Journal of Botany 81:1247–
779 1266.
780Hufford, K. M., and S. J. Mazer. 2003. Plant ecotypes: genetic differentiation
781 in the age of ecological restoration. Trends in Ecology & Evolution
782 18:147–155.

Jacobs, D. F., K. F. Salifu, and J. R. Seifert. 2005. Relative contribution of initial root and shoot morphology in predicting field performance of hardwood seedlings. New Forests 30:235–251.

Kitzmiller, J. H. 2005. Provenance Trials of Ponderosa Pine in Northern California. Forest Science 51:595–607.

Koehler, K., A. Center, and J. Cavender-Bares. 2012. Evidence for a freezing tolerance–growth rate trade-off in the live oaks (Quercus series Virentes) across the tropical–temperate divide. New Phytologist 193:730–744.

Kranabetter, J. M., M. U. Stoehr, and G. A. O'Neill. 2012. Divergence in ectomycorrhizal communities with foreign Douglas-fir populations and implications for assisted migration. Ecological Applications 22:550–560.

Langlet, O. 1971. Two Hundred Years Genecology. Taxon 20:653–721.

Ledig, F. T., and J. H. Kitzmiller. 1992. Genetic strategies for reforestation in the face of global climate change. Forest Ecology and Management 50:153–169.

Little, E. L. 1971. Atlas of United States trees. Volume 1. Conifers and important hardwoods. Miscellaneous Publications. United States Department of Agriculture.

Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. Journal of Biogeography 25:735–742.

Mangold, R. D., and W. J. Libby. 1978. A model for reforestation with optimal and suboptimal tree populations. Silvae Genetica 27:66–68.

Martínez-Berdeja, A., J. A. Hamilton, A. Bontemps, J. Schmitt, and J. W. Wright. 2019. Evidence for population differentiation among Jeffrey and Ponderosa pines in survival, growth and phenology. Forest Ecology and Management 434:40–48.

Marx, D. H., W. C. Bryan, and C. E. Cordell. 1977. Survival and Growth of Pine Seedlings with Pisolithus Ectomycorrhizae after Two Years on Reforestation Sites in North Carolina and Florida. Forest Science 23:363–373.

McDonald, P. M., and G. O. Fiddler. 2010. Twenty-five years of managing vegetation in conifer plantations in northern and central California: results, application, principles, and challenges. Gen. Tech. Rep. PSW-GTR-231. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

McElreath, R. 2016. Statistical rethinking: a Bayesian course with examples in R and Stan. CRC Press, Boca Raton, Florida.

McLachlan, J. S., J. J. Hellmann, and M. W. Schwartz. 2007. A Framework for Debate of Assisted Migration in an Era of Climate Change. Conservation Biology 21:297–302.

Millar, C. I., and W. J. Libby. 1989. Disneyland or native ecosystem: genetics and the restorationist. Ecological Restoration 7:18–24.

Morgenstern, M. 2011. Geographic variation in forest trees: genetic basis and application of knowledge in silviculture. UBC press, Vancouver, British Columbia.

Nalder, I. A., and R. W. Wein. 1998. Spatial interpolation of climatic Normals: test of a new method in the Canadian boreal forest. Agricultural and Forest Meteorology 92:211–225.

Nelder, J. A. 1962. New Kinds of Systematic Designs for Spacing Experiments. Biometrics 18:283–307.

Oleksyn, J., P. B. Reich, W. Chalupka, and M. G. Tjoelker. 1999. Differential Above- and Below-ground Biomass Accumulation of European Pinus sylvestris Populations in a 12-year-old Provenance Experiment. Scandinavian Journal of Forest Research 14:7–17.

O'Neill, G., T. Wang, N. Ukrainetz, L. Charleson, L. McAuley, A. Yanchuk, and S. Zedel. 2017. A proposed climate-based seed transfer system for British Columbia. Technical report 099, Province of British Columbia Forests, Lands, and Natural Resource Operations.

Oyler, J. W., A. Ballantyne, K. Jencso, M. Sweet, and S. W. Running. 2014. Creating a topoclimatic daily air temperature dataset for the conterminous United States using homogenized station data and remotely sensed land skin temperature. International Journal of Climatology 35:2258–2279.

PRISM Climate Group. 2019. http://prism.oregonstate.edu. Oregon State University.

Putten, W. H. V. der. 2012. Climate Change, Aboveground-Belowground Interactions, and Species' Range Shifts. Annual Review of Ecology, Evolution, and Systematics 43:365–383.

852Quinn, G. P., and M. J. Keough. 2002. Experimental Design and Data Analysis
853 for Biologists. Cambridge University Press.
854R Core Team. 2018. R version 3.5.0. R: A language and environment for
855 statistical computing. R Foundation for Statistical Computing, Vienna,
856 Austria.
857Rice, K. J., and E. E. Knapp. 2008. Effects of Competition and Life History
858 Stage on the Expression of Local Adaptation in Two Native
859 Bunchgrasses. Restoration Ecology 16:12–23.
860Roach, D. A., and R. D. Wulff. 1987. Maternal effects in plants. Annual review
861 of ecology and systematics 18:209–235.
862Robeson, S. M. 2015. Revisiting the recent California drought as an extreme
863 value. Geophysical Research Letters 42:6771–6779.
864Savolainen, O., T. Pyhäjärvi, and T. Knürr. 2007. Gene Flow and Local
865 Adaptation in Trees. Annual Review of Ecology, Evolution, and
866 Systematics 38:595–619.
867Schiffers, K., E. C. Bourne, S. Lavergne, W. Thuiller, and J. M. J. Travis. 2013.
868 Limited evolutionary rescue of locally adapted populations facing
869 climate change. Phil. Trans. R. Soc. B 368:20120083.
870Schreiber, S. G., C. Ding, A. Hamann, U. G. Hacke, B. R. Thomas, and J. S.
871 Brouard. 2013. Frost hardiness vs. growth performance in trembling
872 aspen: an experimental test of assisted migration. Journal of Applied
873 Ecology 50:939–949.

Schuler, T. M. 1994. Survival, growth, and juvenile-mature correlations in a West Virginia sugar maple provenance test 25 years after establishment. Research Paper NE-689, United States Department of Agriculture, Forest Service, Northeastern Forest Experiment Station.

Snetsinger, J. 2004. Chief forester's standards for seed use, http://www2.gov.bc.ca/assets/gov/farming-natural-resources-and-industry/forestry/tree-seed/legislation-standards/chief_forester_standards.pdf. British Columbia Ministry of Forests.

St Clair, J. B., N. L. Mandel, and K. W. Vance-Borland. 2005. Genecology of Douglas fir in western Oregon and Washington. Annals of Botany 96:1199–1214.

USGS. 2018. 3DEP products and services: The National Map, 3D Elevation Program, https://nationalmap.gov/3DEP/.

Wadgymar, S. M., and A. E. Weis. 2017. Phenological mismatch and the effectiveness of assisted gene flow. Conservation Biology 31:547–558.

Wang, T., A. Hamann, A. Yanchuk, G. A. O'Neill, and S. N. Aitken. 2006. Use of response functions in selecting lodgepole pine populations for future climates. Global Change Biology 12:2404–2416.

Way, D. A., and R. A. Montgomery. 2015. Photoperiod constraints on tree phenology, performance and migration in a warming world. Plant, Cell & Environment 38:1725–1736.

Weeks, A. R., C. M. Sgro, A. G. Young, R. Frankham, N. J. Mitchell, K. A. Miller, M. Byrne, D. J. Coates, M. D. Eldridge, and P. Sunnucks. 2011.

Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evolutionary Applications 4:709–725.

Wright, J. W. 2007. Local adaptation to serpentine soils in Pinus ponderosa. Plant and Soil 293:209–217.

Ying, C. C., and Q. Liang. 1994. Geographic pattern of adaptive variation of lodgepole pine (Pinus contorta Dougl.) within the species' coastal range: field performance at age 20 years. Forest Ecology and Management 67:281–298.

Tables

Table 1: Characteristics of seedling provenances (i.e., USDA-FS operational seed lots from which planted seedlings originated). Seed lots contain seeds collected from one or more trees from one or more stands within the specified seed zone and elevation band.

Planting site	Species	Seed lot ID	Coll. stands	Trees per stand	Seed zone	Source elev. (ft)	Elev. symb.	# of seedl.	Survival (%)	Source precipitation (mm)	Source tempera (°C)
Klamath	Douglas-fir	5253	16	2	301	4500-5000	H	78	94	1170 - 3986	8.1 - 10.2
		3150	43	3	301	3000-3500	M	57	82	888 - 3732	9.4 - 11.6
		2327	48	4	301	2000-2500	L	72	89	875 - 3184	10.1 - 12.
	Incense cedar	5259	1	4	301	4500-5000	H	63	92	1170 - 3986	8.1 - 10.2
		3569	n/a	n/a	301	3000-3500	M	53	70	888 - 3732	9.4 - 11.6
		4775	2	1	301	1000-1500	L	90	92	857 - 2505	11 - 13.5
	Ponderosa pine	5342	11	3	301	4000-4500	H	85	94	1062 - 3933	8.6 - 10.6
		3536	19	2	301	3000-3500	M	89	65	888 - 3732	9.4 - 11.6
		3529	11	3	301	2000-2500	L	66	83	875 - 3184	10.1 - 12.
Plumas	Jeffrey pine	4619	20	1	523	6000-6500	H	46	98	557 - 2379	6.2 - 10.3
		2895	48	2	523	5000-5500	L	49	100	533 - 2114	7.1 - 11.6
	Sugar	7472	7	1	523	6000-	H	45	98	557 - 2379	6.2 - 10.3

	pine					6500					
		7469	5	1	523	4500-5000	L	45	100	524 - 2037	7.3 - 13.3
San Bernardino	Jeffrey pine	6625	24	1	994	7000-7500	H	130	92	342 - 993	7.5 - 11.3
		7130	n/a	n/a	994	5000-5500	L	138	98	201 - 1001	11.2 - 15.

Note: **Seed lot ID**: the USDA-FS seed lot identification code; **Coll. stands**: number of stands from which seeds in the seed lot were collected (records not available for two seed lots); **Trees per stand**: average number of trees per stand from which seeds in the seed lot were collected (records not available for two seed lots); **Seed zone**: California seed zone (Buck et al. 1970) from which seeds were collected; **Source elevation**: the 500-ft elevation band from which seeds were collected (in feet for consistency with USDA-FS delineations; see Table S3 for elevations in meters); **# Seedl**: the number of experimental seedlings that were followed in this study; **Source precipitation** and **Source temperature**: the range of precipitation (normal total annual precipitation over the 1981-2010 period) and temperature (normal mean annual temperature over the 1981-2010 period) within the source seed zone and elevation band of the seed lot. The high-elevation seed lot of each species is from the same 500-ft elevation band as the planting site (except for ponderosa pine at the Klamath site, which is from the 500-ft elevation band below the planting site). The text “n/a” indicates records not available.

Table 2: Median model coefficient estimates (with 95% confidence intervals in parentheses) for the stem volume model (a) and survival model (b) for each planting site and species combination.

a. Stem volume (cm^3) models

Site	Species	Model coefficient (mean and 95% confidence in			
		Intercept	**Shrub cover**	**Source elev. (L)**	**Source elev (M)**
Klamath	Douglas-fir	**2.95 (2.46, 3.47)**	-0.1 (-0.24, 0.03)	0.25 (-0.01, 0.52)	-0.03 (-0.68, 0.61)
Klamath	Incense cedar	**2.31 (1.81, 2.86)**	-0.01 (-0.14, 0.1)	**0.66 (0.33, 0.95)**	-0.17 (-0.73, 0.37)
Klamath	Ponderosa pine	**3.49 (3.26, 3.74)**	**-0.27 (-0.39, -0.13)**	0.03 (-0.19, 0.27)	0.16 (-0.11, 0.44)
Plumas	Jeffrey pine	**3.3 (2.55, 4)**	**-0.33 (-0.49, -0.19)**	0.28 (-0.33, 0.88)	
Plumas	Sugar pine	**2.92 (2.51, 3.32)**	**-0.23 (-0.36, -0.1)**	0.02 (-0.51, 0.59)	
San Bernardino	Jeffrey pine	**4.01 (3.77, 4.25)**	**-0.65 (-0.75, -0.55)**	**0.44 (0.09, 0.8)**	

b. Survival (%) models

Site	Species	Model coefficient (mean and 95% confidence interval)			
		Intercept		**Source elev. (L)**	**Source elev (M)**
Klamath	Douglas-fir	**2.65 (1.47, 3.84)**		-0.28 (-1.66, 1.09)	-1.09 (-2.58, 0.45)
Klamath	Incense cedar	**3.06 (0.57, 5.7)**		-0.54 (-3.23, 1.8)	**-2.14 (-4.22 0.24)**
San Bernardino	Jeffrey pine	**2.39 (1.75, 2.99)**		**1.44 (0.09, 2.7)**	

Note: Models were fitted using standardized predictor variables (see Methods) to facilitate comparison among coefficients and species. A separate model was fitted for each site-by-species combination. The source elevation coefficients correspond to dummy variables for seed lots (low- and mid-elevation), with high-elevation as the base level incorporated into the model intercept. For pairwise contrasts among seed lots, see Appendix S1: Table S2. Coefficient estimates with 95% confidence intervals that exclude zero are bolded. Coefficients for survival models for Ponderosa pine at the Klamath site and Jeffrey and sugar pine at the Plumas site are not shown because survival was either consistently very high (Plumas species; Appendix S1: Table S1) or because one experimental block contained too few seedlings for robust model fits (Klamath ponderosa pine). AUC: area under the receiver-operating characteristic curve.

Figure legends

Fig. 1: Potential seed collection locations for the high-elevation (purple outline), mid-elevation (blue outline), and low-elevation (green outline) seed lots of incense cedar trees planted at the Klamath site. Potential collection locations are delineated based on the 500-ft source elevation band of each seed lot (Table 1) and additionally constrained by the seed zone (seed zone 301; orange outline) identified in USDA-FS seed lot records. The gray background shading depicts normal mean annual total precipitation for the 1981-2010 reference period (PRISM Climate Group 2019), with lighter shades reflecting higher precipitation. The extent of the main map is outlined in red in the inset map of California. For maps of the other species and planting sites (with elevation instead of precipitation as the background), see Appendix S1: Figs. S1-S6.

Fig. 2: Potential climate space from which seeds in each seed lot may have been collected. Each point reflects a random location from within the region constrained by the seed zone and 500-foot elevation band that each seed lot represents. Each color depicts a different seed lot within each site and species combination. The gray star depicts the climate at the planting site over the 1981-2010 normal period. The orange star depicts the climate at the planting site during the four-year duration of the experiment (October 2011 – September 2015). The high-elevation seed lot of each species is from the same 500-ft elevation band as the planting site, except for Ponderosa pine at the Klamath site, which was from the 500-ft elevation band below the

planting site. Point clouds appear slightly different across seed lots sourced from the same seed zone and elevation band because the points are randomly drawn (see Methods).

Fig. 3: Median model-fitted stem volume (and 95% confidence interval) of the seedlings of each seed lot at the end of the study, following three years of growth in the field. Fitted final stem volume accounts for (and holds constant across seed lots within each site-by-species combination) initial seedling stem volume and shrub competition (see Methods). The high-elevation seed lot of each species is from the same 500-ft elevation band as the planting site (except for Ponderosa pine at the Klamath site, which was from the 500-ft elevation band below the planting site), and the other seed lots were collected from 500 to 3500 ft (~150 to 1050 m) lower in elevation.

Fig. 4: Median model-fitted survival probability (and 95% confidence interval) of the seedlings over three years of growth in the field. Survival of Ponderosa pine at the Klamath site and Jeffrey and sugar pine at the Plumas site are not shown because survival was either consistently very high (Plumas species; Appendix S1: Table S1) or because one experimental block contained too few seedlings for robust model fits (Klamath ponderosa pine). The high-elevation seed lot of each species is from the same 500-ft elevation band as the planting site, and the other seed lots were collected from 500 to 3500 ft (~150 to 1050 m) lower in elevation.

995

Figures

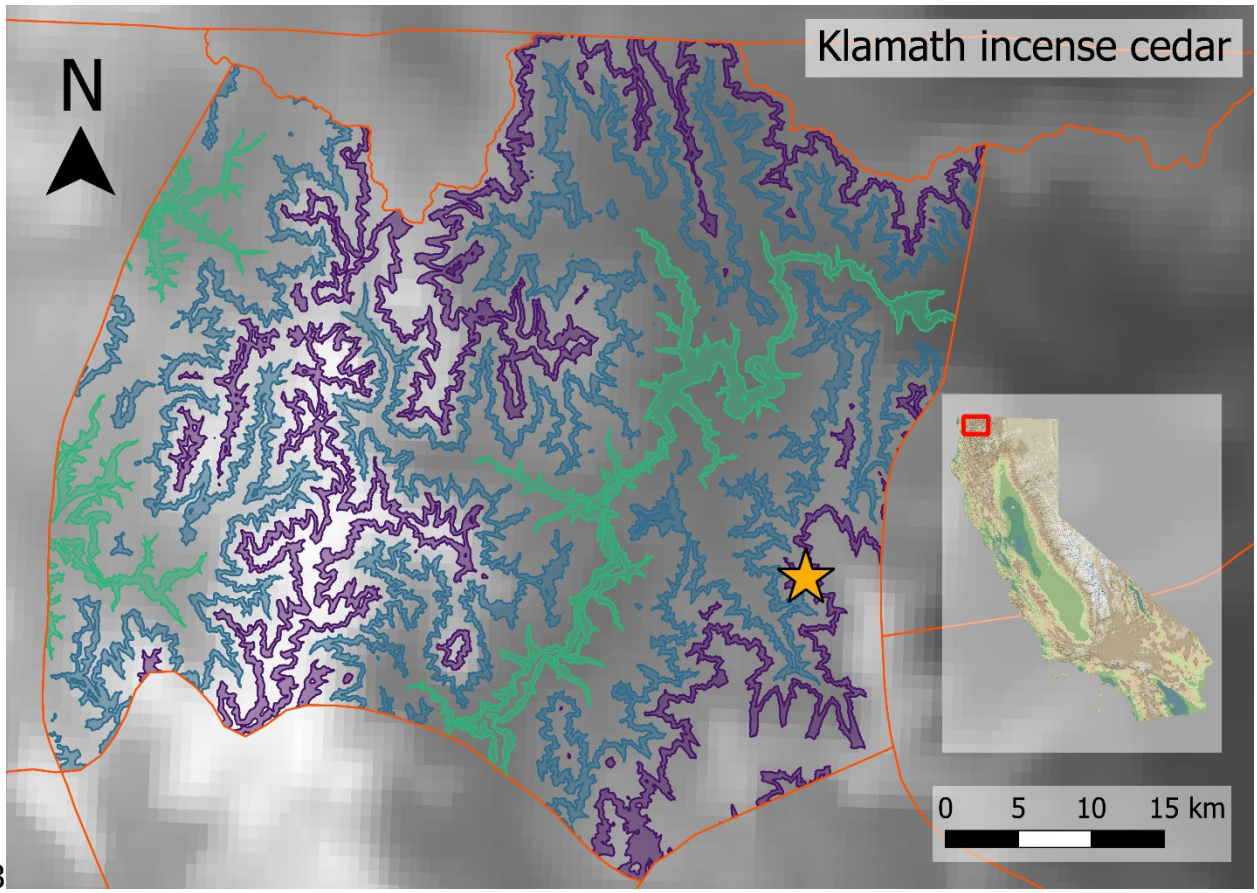


Fig. 1

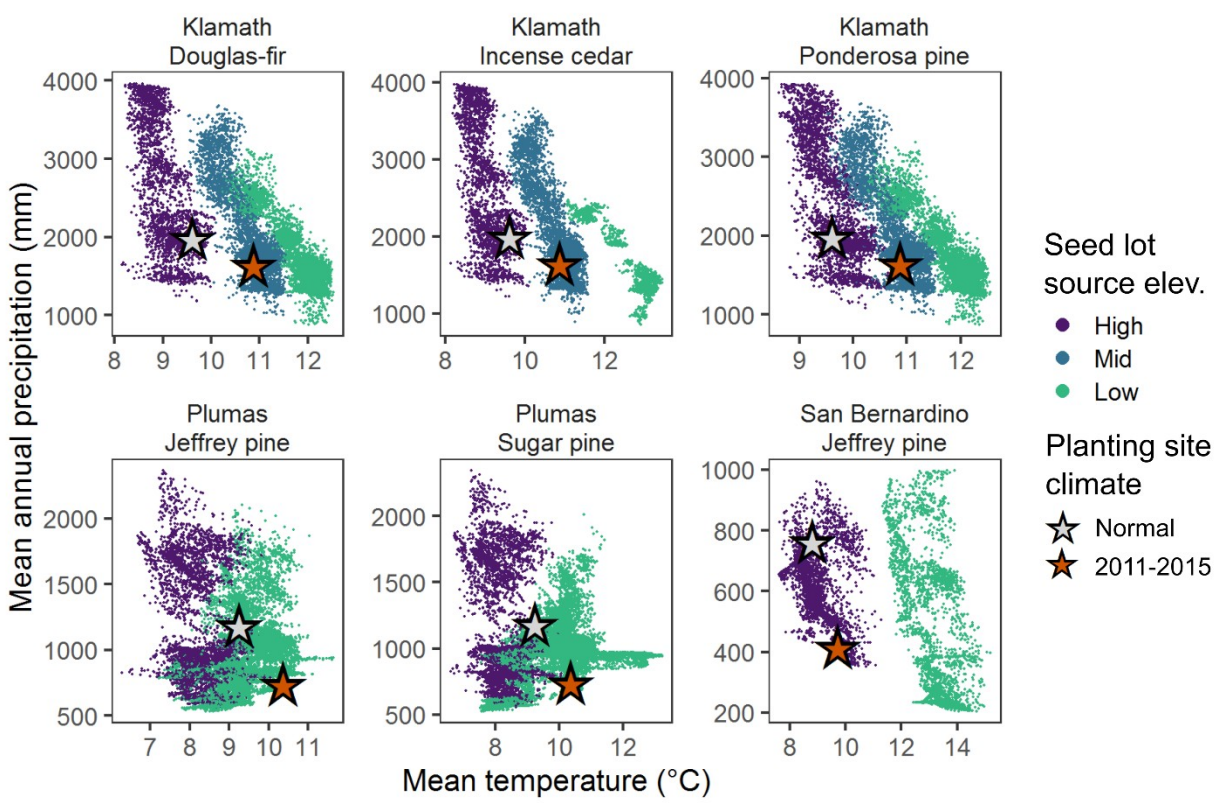
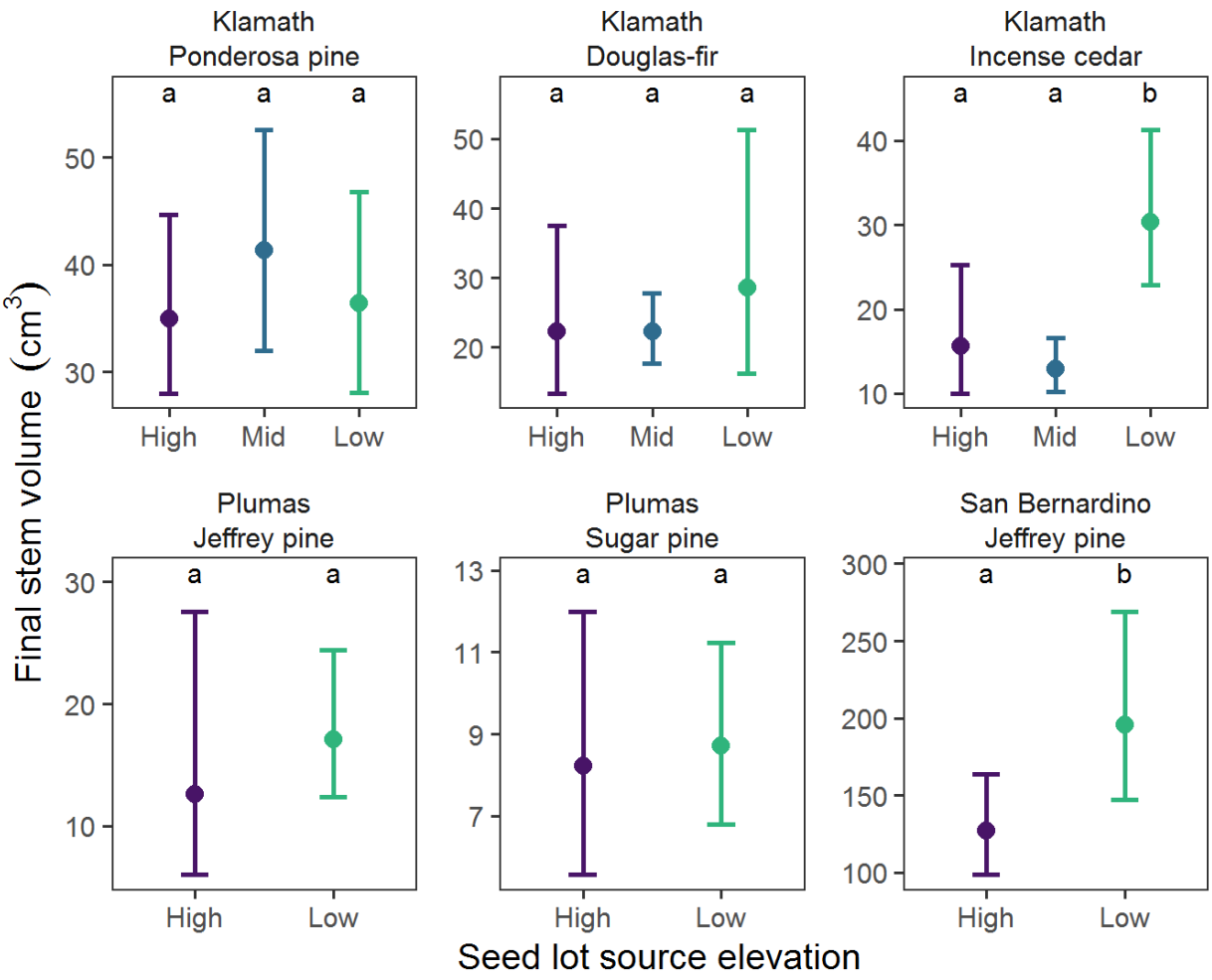
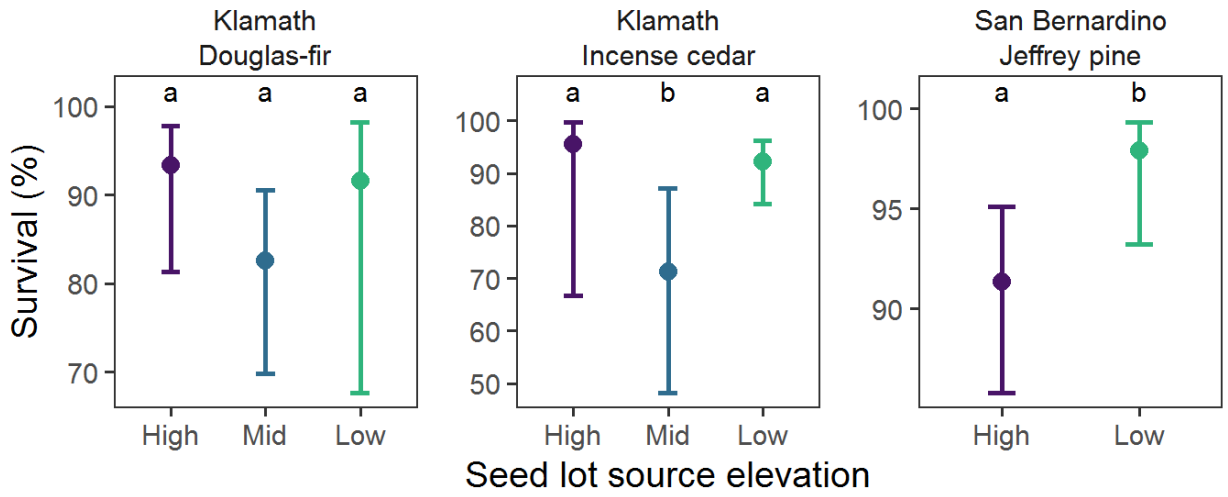

Klamath
Douglas-fir
Klamath
Incense cedar
Klamath
Ponderosa pine
Plumas
Jeffrey pine
Plumas
Sugar pine
San Bernardino
Jeffrey pine
Mean annual precipitation (mm)
Mean temperature (°C)
Seed lot source elev.
High
Mid
Low
Planting site climate
Normal
2011-2015

Fig. 2



1008
1009**Fig. 3**
1010

1011
1012



1013
1014**Fig. 4**
1015